THE FIRST DICYNODONT FROM THE LATE PERMIAN OF MALAGASY

by JEAN MICHEL MAZIN *and* GILLIAN M. KING

ABSTRACT. Until now, no therapsid was known with any certainty from Malagasy. The present specimen, discovered in 1948, but never described, is the first record of a complete dicynodont skull from this country. A description of the skull is given and it is referred to a new species of the genus *Oudenodon*. The rarity of dicynodonts in Malagasy may be because of environmental differences from the adjoining landmass of Africa.

RESUMÉ. La présence de thérapsides à Madagascar n'avait jamais été montrée avec certitude. Le présent spécimen, collecté en 1948 mais jamais décrit, est la première découverte d'un crâne presque complet de dicynodonte dans cette région. Une description du crâne en est donnée et il est attribué à une nouvelle espèce du genre *Oudenodon*. La rareté des dicynodontes à Madagascar peut être due aux conditions de milieu, différentes de celles régnant sur la masse continentale africaine contiguë.

THE Permo-Triassic of Malagasy, sometimes called the 'Malagasian Karoo' is known for the richness of its fossils which have been found in reptile-bearing nodules from the Lower Sakamena Formation (Late Permian), (Piveteau 1926, 1957; Carroll 1981; Currie 1981). Reptiles, such as *Hovasaurus*, *Thadeosaurus*, *Tangasaurus*, and *Claudiosaurus*, are well represented and constitute a typical Malagasian fauna, unknown elsewhere. Until now, except for a fragmentary and unpublished specimen noted by Piveteau (1957), from below the *Cistecephalus* zone and provisionally referred to as a theropsid, the therapsids did not seem to be represented in this fauna. The abundance of diapsids and the rarity of therapsids characterize the Malagasian Karoo in comparison with the South African Karoo, where therapsids are abundant. However, the study of a new specimen, housed in the collections of the Université Paris 6, confirms the presence of therapsids in the Late Permian of Malagasy.

THE MATERIAL

Locality and material

The specimen was collected in 1948 by François Tortochaux, a French geologist then working for the Malagasian Petroleum Company. It consists of a partially crushed skull, coming from a locality whose exact position is unknown, between Ranohira and Benenitra (south Malagasy). The skull was in a calcareous nodule from the upper part of the psammitic sandstone constituting the latest part of the Lower Sakamena Formation (Late Permian) (Text-fig. 1). The matrix has been removed by acid processing. The skull is nearly complete, but dorsoventrally crushed with a broken skull roof (Text-fig. 2). The bone surface is weathered and sutures are indistinct. The anterior part of the snout is slightly distorted by shear, and the posterolateral part of the right temporal fenestra is preserved only as a film of bone. The total length of the specimen is 160 mm, and the maximal width is 95 mm. The lower jaw is mostly complete and preserved *in situ*. The lateral bones of the right ramus and of the posterior part of the left ramus are missing. In the palate, the pterygoids and right basioccipital tuber are visible. The anteriormost part of the palate is not visible. The atlas, axis and three succeeding vertebrae are also preserved.

Description

In dorsal view, the pre-orbital region is short in comparison with the post-orbital, even allowing for distortion (Text-fig. 3a). The *postorbitals* are large and rise to form a low sagittal crest ending at the level of the pineal foramen. Anteriorly, they are separated by a small shield-shaped *preparietal*. They constitute the anterior and

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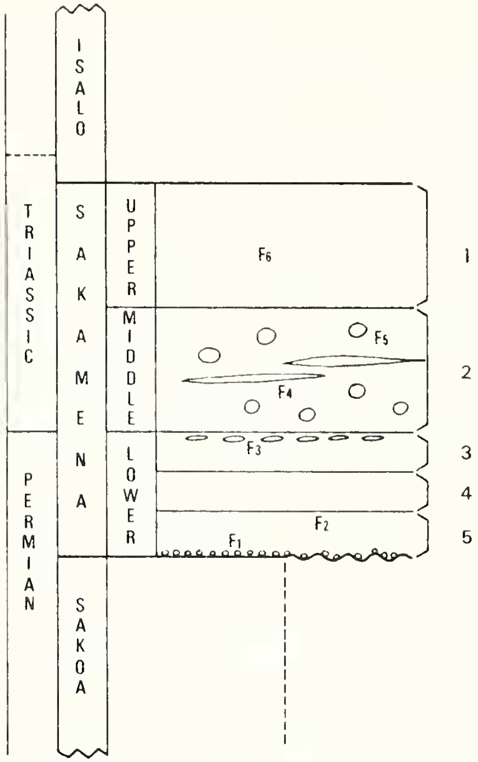


TEXT-FIG. 1. Stratigraphical scale of the Sakamena Formation, with locations of the different fossil levels. 1, clays and sandstone called 'Upper continental red level'; 2, Septaria clays with interbeds of sandstone; 3, psammitic sandstone; 4, clays with gypsum; 5, sandstone and conglomerate. F1, small amphibian and reptile bones; F2, nodules with reptiles; F3, shales with *Glossopteris*, *Voltzia*...; F4, lens of sandstone with small amphibian and *Saurichthys* remains; F5, nodules with fishes; F6, rare plant remains. The dicynodont fossil comes from the level F2.

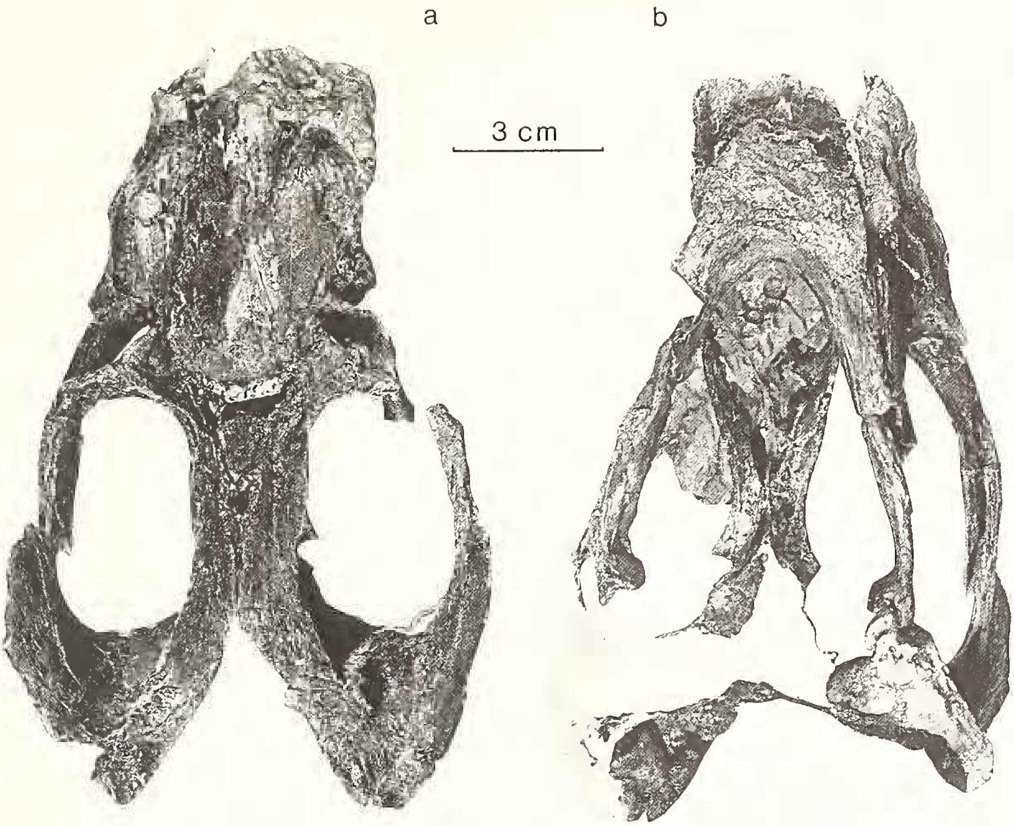
medial border of the temporal fenestrae, and all of the posterior edge of the orbital opening. The *squamosals* are very large, forming the posterior and lateral borders of the temporal fenestrae. Because the skull roof is damaged, the *postfrontals* are not visible, but their impression persists as a depression. They were elongated, with a triangular shape, and seem to have contacted only the postorbitals. The left *prefrontal* persists as an elongated bone bordering the anterosuperior edge of the orbital opening. The *frontals* seem to be large, but their anterior limits cannot be determined. Likewise, the narinal area cannot be observed because of the anterior distortion and loss of the snout. The measurements of the temporal fenestrae are as follows: left: length, 58 mm; width, 30 mm; right: length, 59 mm; width, 31 mm.

In lateral view, the general outline of the skull is modified by the dorsoventral crushing (Text-fig. 3*c*). The specimen is totally edentulous. The *maxilla* is large and extends vertically. The *jugal* is anteroposteriorly elongated, forming the inferior and posterior edges of the orbital opening. The *mandible* is strong, with a thick and high anterior part composed of the *dentary*. Posteriorly, the mandible is thinner. The *articular* is divided into lateral and median articulatory condyles.

The ventral view is more difficult to observe (Text-fig. 3*b*). The palate is largely damaged, and the posterolateral part of the skull is destroyed. The mandibular symphysis is strong and anteriorly extended. Conversely, the posterior part of each ramus is narrow.

Identification

The short snout, elongate temporal fenestra, large laterally-expanded squamosal, and distinctive articular confirm that this specimen is a dicynodont. Among the dicynodonts, this specimen can be compared with the four main Permian genera: *Dicynodon*, *Oudenodon*, *Diictodon* and the rare *Kingoria* (Cluver and Hotton 1981). Because of the lack of a caniniform tusk, it cannot belong to *Dicynodon*. The absence of the distinctive square caniniform process indicates that the specimen does not belong to the genus *Diictodon*. To distinguish between *Oudenodon* and *Kingoria*, it is necessary to know the state of certain characters of the lower jaw, in particular whether a dorsal dentary sulcus is present or not. The present specimen does not have the anterior dorsal surface of the jaw ramus completely exposed, but the dorsal edge of the dentary which is visible is sharp-edged



TEXT-FIG. 2. *Oudenodon sakamenensis*, Late Permian, south Malagasy. Type specimen, PVHR 288. *a*, Dorsal view; *b*, ventral view.

as would be expected of the medial wall of a dorsal dentary sulcus, as present in *Oudenodon*. Another feature which indicates an assignment to *Oudenodon* is the suggestion of a large palatal exposure of the palatine bone. This would be small in *Diictodon* and *Kingoria*.

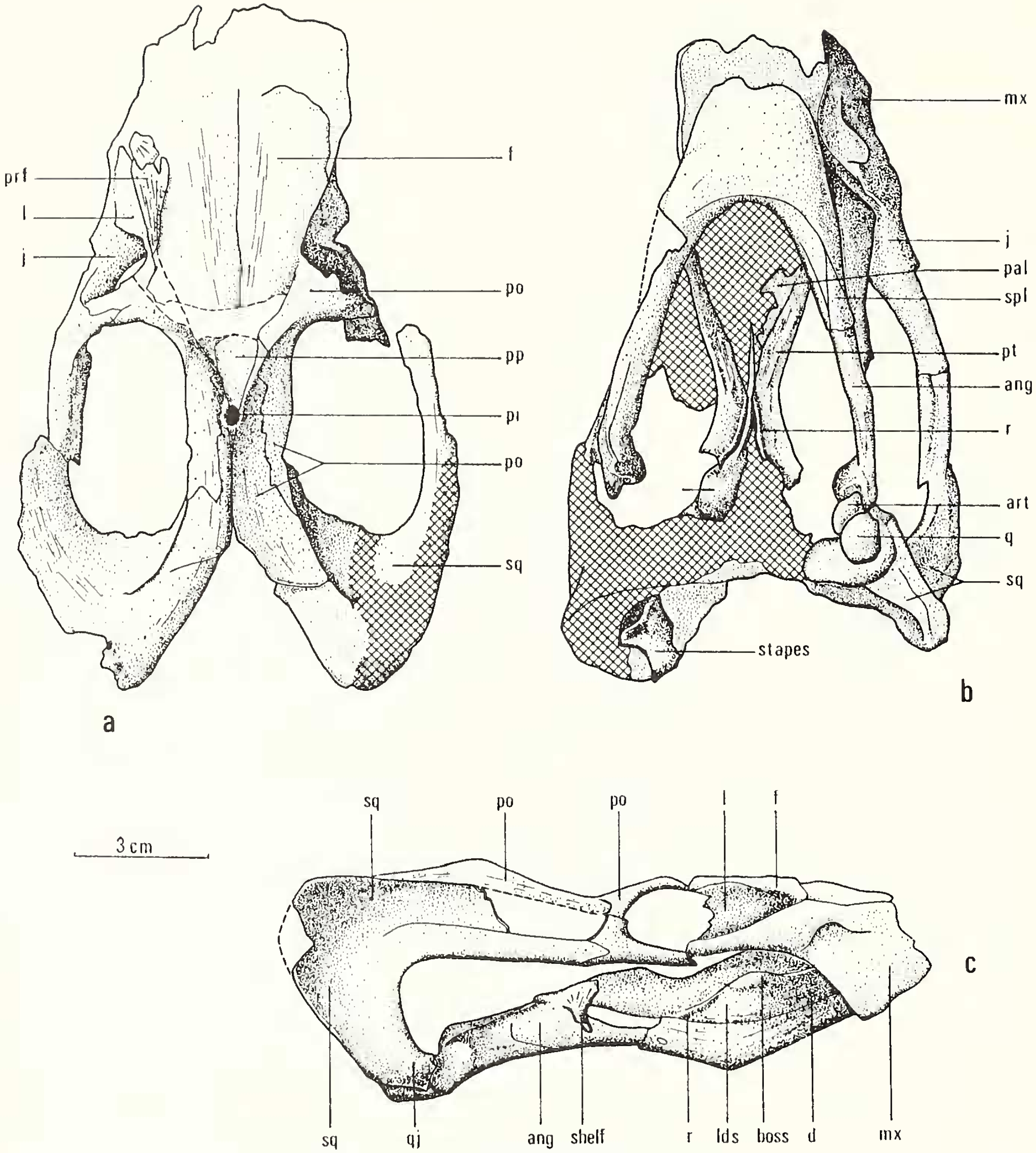
King (1988) lists three species of *Oudenodon*. The genotype is *Oudenodon bainii* Owen, 1860, known from South Africa. *O. grandis* (Haughton 1917) is also from South Africa, while *O. luangwensis* (Boonstra 1938) is known from Zambia (Keyser 1975).

The present specimen presents two features which distinguish it from the known species of *Oudenodon*. First, the lateral dentary shelf is drawn up into a pronounced boss anteriorly which is continued postero-ventrally as a sharp ridge (Text-fig. 3*c*). Secondly, the posterior edge of the mandibular fenestra is drawn up into a blunt ridge oriented antero-ventrally, forming an anterior shelf to the reflected lamina of the angular (Text-fig. 3*c*). On account of these features the present specimen is assigned to a new species of *Oudenodon*.

SYSTEMATIC PALAEONTOLOGY

Suborder ANOMODONTIA Owen, 1859
Infraorder DICYNODONTIA Owen, 1859
Superfamily PRISTERODONTOIDEA Cluver and King, 1983
Family DICYNODONTIDAE Cluver and King, 1983
Subfamily CRYPTODONTINAE Owen, 1859
Genus *Oudenodon* Owen, 1860

Diagnosis. Given by King (1988).



TEXT-FIG. 3. *Oudenodon sakamenensis*, Late Permian, south Malagasy. Type specimen PVHR 288. *a*, Dorsal view; *b*, ventral view; *c*, right lateral view.

Oudenodon sakamenensis sp. nov.

Text-figures 2 and 3

Etymology. From Sakamena, the name of the Formation and of the river which crosses this area.

Holotype. Nearly complete skull, PVHR 288, preserved at the Laboratoire de Paléontologie des Vertébrés de l'Université Paris 6.

Type locality. Between Ranohira and Benenitra, South-western Malagasy.

Horizon. Top of the Lower Sakamena Formation, Late Permian.

Diagnosis. Medium to small member of the genus, skull longer than broad. Lower jaw with lateral dentary shelf drawn up into a boss anteriorly and extending postero-ventrally as sharp-edged ridge; reflected lamina of angular bearing a pronounced blunt shelf anteriorly.

PALAEOBIOGEOGRAPHICAL SIGNIFICANCE

Dicynodonts are known from South Africa, eastern Africa, Morocco, India, China, Antarctica, Europe, USSR, and North and South America, but until now had not been reported from Malagasy. *Oudenodon* is known from South Africa, Zambia and, now, Malagasy. In South African localities, dicynodonts are very abundant fossils, and *Oudenodon* is a common genus from *Cistecephalus* Zone localities, and even more so in the succeeding *Daptocephalus* Zone (King 1986). It is therefore puzzling that these abundant therapsids should be found so rarely in the otherwise reptile-rich fauna of Malagasy.

Two alternative explanations present themselves. First, that Malagasy was separated from South and East Africa by some kind of barrier (sea, mountain) during the Late Permian, preventing easy migration of dicynodonts to Malagasy. In this case, an impoverished dicynodont fauna, composed of species very distinct from the mainland forms, would be expected. This explanation can be dismissed for two reasons. First, it is known that Malagasy was part of the same landmass as Africa during the Late Permian. There was no ocean barrier to migration, and no evidence of other kinds of barrier. Secondly, although the present Malagasian dicynodont is specifically distinct from mainland African forms, it is not particularly different, and no more different than is the Zambian *Oudenodon* from the South African.

The second explanation to account for the rarity of therapsids in Malagasy is that the conditions of fossilization there were very different from those in South Africa. This has been suggested by Piveteau (1926), Currie (1981) and Carroll (1981). This would imply that the habitats in which dicynodonts and other therapsids were abundant in South Africa were not those habitats which have been sampled in the Malagasian sediments. There are some indications that some of the Malagasian diapsids coming from the same locality (*Hovasaurus*, *Claudiosaurus*) were aquatic or semi-aquatic (Currie 1981; Carroll 1981; de Buffrénil and Mazin 1989), and it may, therefore, be that dicynodonts were occupying more terrestrial environments which are not sampled in these Malagasian localities. By contrast, South African localities, where no similar small diapsid assemblages are known, may represent the more terrestrial (or less aquatic) habitats. Further sedimentological and palaeontological sampling of contemporaneous localities in Malagasy, and functional anatomical study of the fossils they contain, is needed before this conclusion can be substantiated.

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ABBREVIATIONS USED IN TEXT-FIGURES

ang: angular; art: articular; b.o.t.: basioccipital tuber; d: dentary; f: frontal; FT: temporal fenestra; j: jugal; l: lachrymal; l.d.s.: lateral dentary shelf; mx: maxilla; ORB: orbital opening; pal: palatal; pi: pineal foramen; po: postorbital; pp: postparietal; prf: prefrontal; pt: pterygoid; q: quadrate; qj: quadratojugal; r: ridge; spl: splenial; sq: squamosal.